A CONTRIBUTION TO THE MORPHOLOGY OF PYRULA.

BY BURNETT SMITH.

INTRODUCTION.

At the present day the genus *Pyrula*[1] is made up of a small number of species and these, though differing from one another somewhat, are nevertheless all very much alike. The thin shell, cancellated sculpture, low spire and long anterior siphon are common to them all. There is no exaggeration in saying that nowhere among the marine gastropods do we find a set of species which are with better reason arranged in one generic group. They are indeed distinctly monophyletic. On examining the fossil Pyrulas we find that the genus gives us a homogeneous series of species ranging back in time well into the Eocene. It is true that *Pyrula* is seldom a common fossil in any formation, and likewise it does not furnish us with great series of closely related races which follow one another in the rocks of any continuous geological section. Nevertheless the very homogeneity of the scattered fossil species comes to our aid. Their distinctly peculiar shell characters are always present, just as in the widely distributed living forms.

The desire to deal with a group whose monophyletic nature is above suspicion has led the author to exclude from the present paper many Eocene and earlier species which are usually assigned to the genus. Not a few of these may be indeed very close to *Pyrula*, but the present paper has for its object the recording of the changes which a monophyletic assemblage of species actually exhibits when we trace its members through the different episodes of the time range and from one geographical province to another. Still other early species appear to be referable to *Pyrula*, but the preservation of the specimens is not good, and this is an essential for a proper understanding of the shell sculpture and apical characters. These forms also must be omitted.

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[1] This paper is intended merely as a study of some of the morphologic changes in a monophyletic group and makes no pretense of being a systematic revision of the genus. Most of the specific types are either undesignated, lost or unavailable, and the author has learned by experience that the average published figure of a species of *Pyrula* is extremely unreliable. For these reasons the propriety of using the generic name *Pyrula* is not here considered, and the classification in Tryon's *Manual of Conchology* has been followed in discussing the recent forms. In dealing with the fossil species references are given in each case.

Morphology.

Among the species of *Pyrula* (as here restricted) the similarity of their grosser morphologic features is evident at a glance. The shell is always light and thin, the whorls are as a rule very evenly rounded and always increase rapidly in size, the spire is low and each whorl rises high on its predecessor. This latter feature often makes the top of the shell appear quite flat. Contrasted with the low spire, the branchial siphon is much produced anteriorly and often slightly curved. The shell is, in fact, roughly pear-shaped.

It is, however, only when the finer features of the ornamentation are studied that we realize the unusual constancy of the genus. The early whorls are smooth, and this smooth stage may occupy from one (or even less than one) to two and three-quarters or even three whorls.[2]

The smooth stage is followed rather sharply by the fine ribs and spirals of the cancellated stage. Perhaps, on the whole, the spirals appear a little earlier in life than do the ribs, but this is not a marked feature. The cancellated stage persists in all the species to the end of shell growth. At first there is but one set of spirals, but later secondary sets appear between the primary spirals. Still finer sets of spirals are introduced with the course of the ontogeny. Sometimes by the end of the last whorl the secondary and later spirals may have acquired about the same strength as the original primary spirals, though it is more common for the primary spirals to be strongest, with the other sets fainter and fainter according to the order in which they are introduced into the ontogeny, the last sets introduced being faintest. On their first appearance the ribs and the primary spirals are of about equal strength, but in the later whorls the primary spirals are as a rule considerably stronger than the ribs. Exceptionally the ribs on the later whorls may be as strong as the primary spirals.

To give any idea of the morphologic features which now serve, and have in the past served, to differentiate the species we must employ unusual methods. Ordinary descriptions fail to convey the meaning. It has therefore been thought best to use tables for the purpose. In these tables the two major ontogenetic stages are represented by the letter A for the smooth stage and B for the cancellated stage. These stages are marked off on the line of the ontogeny as they appear in the different whorls. The numbers stand for the whorls.

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[2] Sections of the apex in *P. papyratia* Say, show that it is filled with a secondary limy deposit.

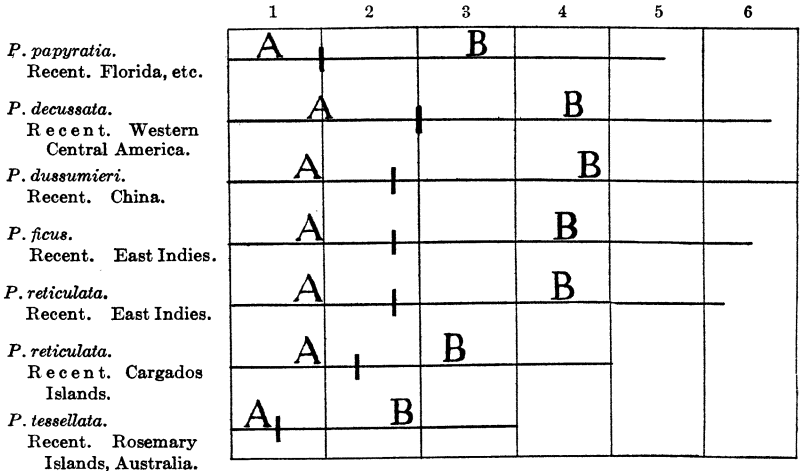

TABLE I.

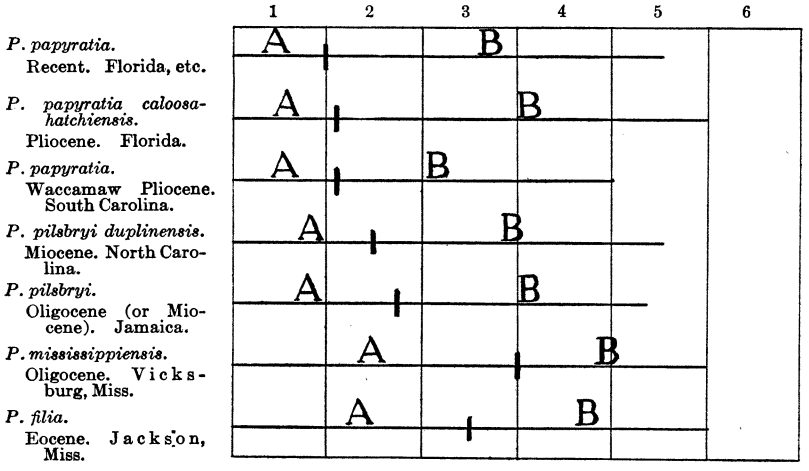

TABLE II.

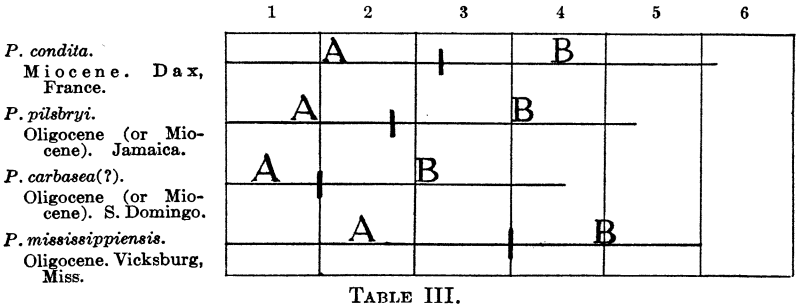

TABLE III.

Table I gives a representation of the ontogenetic features of the recent species. *Pyrula decussata* Wood and *Pyrula ficus* Linn. are the most clear-cut and distinctive species as regards the ornamentation in the cancellated stage. *Pyrula decussata* is distinguished by its strong primary spirals, while *P. ficus* has flat, weak spirals and very faint ribs. *Pyrula dussumieri* Valenc. is marked by its long slender form and the relatively high spire. In their apical features *Pyrula decussata, P. ficus* and *P. dussumieri* are all very much alike. The smooth stage occupies about 1.6–2 whorls and these early whorls are small.

Among the forms commonly grouped as *Pyrula reticulata* Lam. there is much variation. How much of this is individual and how much racial or specific it is impossible to say with the present data. They all have relatively strong ribbing, and this together with spirals of about the same strength gives them a much more conspicuously cancellated appearance than is seen in any other recent species. In this *Pyrula reticulata* assemblage the smooth stage occupies from 1.3 to 1.75 whorls and the first whorl varies not a little in size. These forms strongly recall *Pyrula condita* Brongniart[3] of the European Miocene in the sculpture of the cancellated stage. It is probable that more accurate collections will necessitate the division of *P. reticulata* into separate geographical races or species.

Pyrula tessellata Kobelt is a small type which differs from all others in the peculiar character of its apex. The cancellated stage has been thrown so far back in the ontogeny that little more than the globular beginning of the first whorl is smooth. This smooth portion is large and swollen. In fact *P. tessellata* is, in its apical characters, the most abnormal of any of the Pyrulas.

On comparing *Pyrula papyratia* Say with the other species we find that it is essentially similar to them as regards its cancellated stage. When, however, the apex is examined it is seen to be sharply distinguishable from all other recent forms. The smooth stage is restricted to about one whorl and this whorl is large and swollen. In this respect *P. papyratia* is only surpassed by *P. tessellata.*

Table I demonstrates clearly that we may have living at one time on the earth's surface a number of very closely related forms which show markedly different degrees of acceleration and much variation in the apex.

Table II illustrates the changes shown by some of the American

[3] See Cossmann, *Essais de Paléoconchologie Comparée*, pt. V, pl. VI, fig. 7.

species when they are traced from the Jackson Eocene down to the present time. To obtain a good idea of this series it is perhaps best to consider first the more recent forms. As stated above, the living *Pyrula papyratia* is chiefly notable for its large and swollen apex, the smooth stage being confined to one whorl. The cancellated stage is in no way unusual.

To find an ancestor for the *Pyrula papyratia* of Florida seas we naturally look in the Pliocene of the Gulf and other Southern States. A form which has been referred to *P. papyratia*[4] is furnished by the Floridian Pliocene, and another shell from the Pliocene Waccamaw beds of South Carolina has been likewise regarded as specifically identical with it. A critical study of the Florida Pliocene form demonstrates that it is extremely close to the recent species. In fact its cancellated stage is similar in every respect. The apex is likewise almost the same, but differs in having the cancellated stage begin a little later in the ontogeny. The first whorl is also perhaps a trifle smaller in the fossil form. Altogether this Florida Pliocene type is specifically identical with the recent *P. papyratia*. Nevertheless the author believes that it may with propriety be designated as the subspecies *Pyrula papyratia caloosahatchiensis*. The Waccamaw Pliocene forms have an apex similar to that of *P. papyratia caloosahatchiensis*. The individuals examined are, however, all immature, and it is therefore impossible to note the sculpture of the later cancellated stage. It is probable that a better series of specimens will establish the identity of this race with the one from the Florida Pliocene.

In the Miocene beds of the United States *Pyrula* appears to be a rather uncommon fossil. From the Calvert Miocene of Maryland Martin has described *Pyrula harrisi*.[5] He says that good examples are rare. I have had no opportunity to examine specimens of this species, but it appears from the figure to be well removed from the *P. papyratia* stock. In the very full collection of the Wagner Free Institute of Science (Philadelphia) is a specimen collected in Duplin County, North Carolina, by Mr. Charles W. Johnson. It has been referred to *P. papyratia*. On a close examination of this form, however, it is evident that we must assign to it a separate specific name. It is also plainly distinct from the Maryland *P. harrisi*. It is by its apical characters that this North Carolina species is distinguished from the Pliocene and recent *P. papyratia*. The smooth stage occupies about 1.5

[4] See Dall, *Trans. Wag. Inst.*, III, p. 163.
[5] *Md. Geol. Surv. Miocene*, p. 226, pl. LV, fig. 3.

whorls and the first whorl is small, and not large and swollen as in *P. papyratia.* In these respects it is more closely allied to most other Miocene forms and to some of the recent species of the Indo-Pacific region. It is especially near to the form from the Oligocene (or Miocene) beds of Santo Domingo which Gabb[6] refers to *P. papyratia.* I have examined Gabb's specimens and find them to be identical with the better preserved forms from the Oligocene (or Miocene) beds of Bowden, Jamaica. In their apical characters they are all clearly distinct from *P. papyratia.* I have selected the Bowden race as typical of this new species; the type specimen for the following description being one of the lot numbered 11,144 in the collection of the Academy of Natural Sciences of Philadelphia.

Pyrula pilsbryi n. s.

Locality.—Bowden, Jamaica, W. I.

Horizon.—Bowden beds, Oligocene (or Miocene).

Whorl 1.—Smooth and rounded.

Whorl 2.—Smooth and rounded for about one-half or three-quarters of a whorl, and then the cancellated stage with its fine ribs and spirals sets in.

Whorl 3.—Cancellated stage. Fine ribs and spirals.

Whorls 4, 5.—Cancellated stage, with secondary sets of spirals

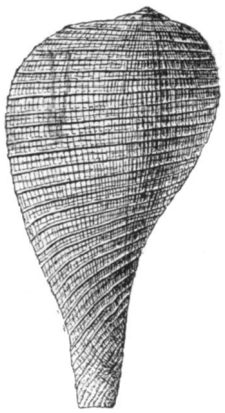

Fig. 1.—*Pyrula pilsbryi* n. s. Bowden beds. Bowden, Jamaica. Length = 42 mm.

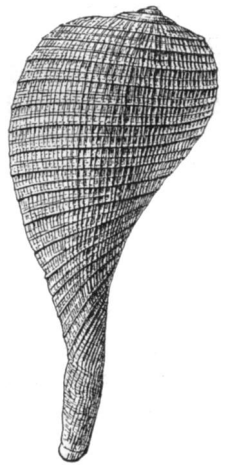

Fig. 2.—*Pyrula pilsbryi duplinensis.* Miocene. Duplin County, North Carolina.

[6] "Topography and Geology of Santo Domingo," *Trans. Am. Phil. Soc.,* Vol. 15, p. 223, 1881.

introduced between the primary spirals. Other still finer spirals are introduced with the progress of the ontogeny. The primary spirals are the strongest, while those sets of spirals introduced latest are weakest.

Remarks.—P. pilsbryi is much like the Duplin form in its apical features, but differs from it in the relatively weaker primary spirals which do not dominate the later intercalated spirals to any great extent. For the North Carolina form the name *Pyrula pilsbryi duplinensis* is here proposed.

The Vicksburg species *Pyrula mississippiensis* Conrad,[7] it will be noticed, has the first three whorls occupied by the smooth stage. The first whorl is also smaller than in *P. pilsbryi.*

In the Jackson Eocene a species, probably *Pyrula filia* Meyer,[8] has, like the Vicksburg form, a small first whorl and the smooth stage takes up at least 2.5 whorls. It is a little more accelerated than the later Vicksburg species. This emphasizes the fact that a less accelerated and specialized race does not always underlie the more specialized race.

Nevertheless we can say that on the whole Table II shows us a gradual acceleration of the features of the cancellated stage as we trace the different types from the Eocene to the present day. This acceleration is accompanied by a gradual enlargement of the first whorl until we reach the culmination of this feature in the recent *Pyrula papyratia.*

Another exception to this gradual development is furnished by the form from the Santo Domingo Oligocene (or Miocene) which Gabb referred to *Pyrula mississippiensis.* This reference[9] is entirely incorrect, for Gabb's specimen has a very large swollen apex with not more than one smooth whorl. It is fully as accelerated as *P. papyratia* in this respect, but it cannot be ancestral to the recent species on account

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[7] See *Ficus mississippiensis* Con., *J. Acad. Nat. Sci. Phila.*, 2d ser., Vol. 1, p. 117.

[8] *Bericht über Senckenbergische naturforschende Gesellschaft in Frankfurt a. M.*, 1887, *Ficula filia* Meyer, p. 8, Taf. I, fig. 10. I make this reference with some doubt.

[9] See Gabb, in *Trans. Am. Phil. Soc.*, Vol. 15, p. 223. Gabb considered Guppy's *Ficula carbasea* as a synonym for Conrad's *Ficus mississippiensis.* He says: "I have compared Mr. Guppy's shell with Mr. Conrad's original specimens from Vicksburg, Mississippi, and find them identical in form and sculpture. I am by no means sure that this should not be considered the same as *F. decussatus* (*F. ventricosus*), the common west coast Mexican form."

It can, of course, be neither *P. mississippiensis* nor *P. decussata,* and as it resembles Guppy's figure I have referred it to *P. carbasea.* Guppy's type I have not seen.

of the great strengthening of its primary spirals. In this respect it resembles the Panamic *P. decussata.* The unspecialized apex of *P. decussata* is, however, sufficient to preclude a derivation from this fossil Santo Domingan form. Altogether this latter appears to be an early departure from the stock of the generalized Pyrulas of the Oligocene and Miocene. It probably has no descendants in later beds. I have referred it with some doubt to *Pyrula carbasea* Guppy.[10]

Table III shows that the apex was as variable in the Eocene, Oligocene, and Miocene as at the present day. The great length of the smooth stage and slight acceleration of the cancellated stage are noteworthy features of this group of species. It is only in *P. carbasea*(?) that the smooth stage is short and restricted.

Range and Distribution.

The genus *Pyrula* as restricted in this paper ranges from the late Eocene to the present day. Earlier in the Eocene we encounter an abundance of forms which appear to be closely related to the species here considered. Their inclusion in the present study would, it is believed, throw some doubt on the monophyletic nature of the group. Their consideration is therefore delayed, so that we may be able to observe the changes in a series which obviously can be referred to only one generic stock.

In the Jackson Eocene and in the later Vicksburg beds the species are remarkable for the great length of the smooth stage and for the small size of the early whorls. The same characteristics are also to be observed in the European Miocene *Pyrula condita.* The three species *P. filia* of the Jackson Eocene, *P. mississippiensis* of the Vicksburg beds, and *P. condita* of the Miocene of Europe all exhibit similar apical features. They represent the most primitive expression of the *Pyrula* assemblage which the geological record furnishes.

In the Oligocene (or Miocene) deposits of Bowden, Jamaica, we find *Pyrula pilsbryi,* and in the Miocene of North Carolina occurs *P. pilsbryi duplinensis.* Both are very much alike as to the characters of the smooth stage. In them it is more restricted than in *P. condita* or in the American Vicksburg and Jackson types. In other words, the cancellated stage is thrown farther back into the ontogeny. In addition, the early whorls have now become larger in size. Altogether *P. pilsbryi* is very similar in its early whorls to *P. decussata, P. dussumieri, P. ficus,* and some specimens of *P. reticulata.* These three latter species

[10] *Ficula carbasea Q. J. Geol. Soc. Lond.,* 1866, Vol. 22, p. 580.

are living to-day in the Indo-Pacific region. In its apical features, then, *P. pilsbryi* has attained about the same evolutional grade as several of the recent forms.

Nevertheless there is in the Oligocene or Miocene at least one exception to the general prevalence of the primitive apex. This is furnished by the *Pyrula carbasea*(?), which in addition to the feature already mentioned has a specialized adult sculpture that marks it as an early offshoot from the main stock, and it is probably also a terminal member of such an offshoot.

Passing over this aberrant form, we find that in the Pilocene rocks of North America the smooth stage is still further restricted and the apex yet larger, for there is at least one subspecies of *Pyrula papyratia*. It is more primitive than the recent *P. papyratia*, for the first whorl is hardly as large and the cancellated stage is not quite so accelerated as in the recent form. It is very close and must be regarded as ancestral to *P. papyratia* of the modern Florida seas.

In American rocks, then, we have an excellent series showing the gradual acceleration of the sculpture and the increase in size of the early whorls. With the exception of *P. mississippiensis* and *P. carbasea* this American series represents a good morphological succession, and from *P. pilsbryi* to the living *P. papyratia* we can reasonably assume a phylogenetic succession as well.

The solution of the ancestry for the present day species of the Indian and Pacific Oceans can hardly be attempted with the meager data at our command. *Pyrula decussata, P. dussumieri,* and *P. ficus* probably owe their origin to some such generalized types as we have seen in the American Eocene and the European Miocene. Just how long their separate specific stocks have been distinct it is impossible to say. The forms described as *P. reticulata* probably represent a group of geographical races which have arrived at different stages of evolution. Some of them are very like *Pyrula condita* of the Miocene, for the ribs are strong and, equalling the primary spirals, impart a markedly cancellated appearance to the shell. *Pyrula tessellata* of Australian seas represents an offshoot from the primitive stock. It has become distinctive by its large swollen apex and the encroachment upward of each whorl high on its predecessor; but its ribbing is relatively strong, the sculpture of its cancellated stage being primitive.

A point of great interest is the succession of morphological features which has taken place in the Gulf and Caribbean region with the progress of the Tertiary. *Pyrula pilsbryi* is more specialized than the Eocene forms, but less specialized than the later races which are

grouped together as *P. papyratia*. When we compare *P. pilsbryi* with *P. decussata* of the Panamic geographical province we find that the Pacific form is distinct in its later whorls, but very similar to the fossils in the characters of its apex.

Altogether this evidence points to free communication between the Atlantic and Pacific basins during Miocene time, a time when most Pyrulas possessed the primitive type of apex. With the end of the Miocene this strait between the two oceans was closed by the elevation of the land bridge which has ever since connected the continents of North and South America. From the time when this barrier was interposed down to the present the forms of the Caribbean and Gulf regions have undergone a striking evolution, marked by the accleration of the cancellated stage and the enlargement of the initial whorl. On the other hand, the forms inhabiting the waters on the Pacific side of the isthmus have retained the ancient apical features of the Miocene.

Summary.

The assemblage of forms treated in this paper is particularly well adapted for showing the mutations and variations of a gastropod stock. In order that the results may be of value it is essential that the group be a restricted one. *Pyrula*, or at least that part of the genus here considered, fulfills the above conditions. The distinctions between its species are so slight, and they are all so unlike the examples of other genera, that we may well feel that they constitute a single genetic stock.

In addition to the slight but more apparent specific differences furnished by the cancellated stage we have the differences exhibited by the apices. If we trace the members of the genus back into the Tertiary, we find every gradation between the two extremes of apical modification.

The more important changes which have taken place since the late Eocene are found not so much in the adult sculpture as in the features of the apex. We have, especially in America, a regular series, beginning with forms having a smooth stage of two or three whorls, followed by species in which the smooth stage is more restricted, and finally terminating in *Pyrula papyratia* of Gulf and Caribbean waters, whose smooth stage does not persist beyond the close of the first whorl. This change from the two- or three-whorled smooth stage to the one-whorled smooth stage is accompanied throughout by the gradual enlargement of the early whorls. The more restricted the smooth stage becomes the larger grows the initial whorl.

If we examine the recent species of *Pyrula*, we find here again different apical characters which can usually be duplicated in the fossil forms of the American rocks. For instance, though their adult sculptures may differ, the recent species *P. decussata* and *P. dussumieri* and the Oligocene (or Miocene) *P. pilsbryi* all possess a very similar style of apex.

At the present day the genus is widely distributed in the shallow waters of the tropical seas. Though these seas are now separated by land barriers, it is probable that in Eocene, Oligocene and Miocene times the marine connections between the different provinces were much more prominent features of the geography. Then, in all likelihood, the genus had a continuous distribution around the world; and even where land barriers were interposed near the equator, it is probable that a more generally moderate climate enabled its representatives to pass through latitudes where now their existence would be impossible.

The differences between *Pyrula dussumieri* of China and *P. decussata* of the west coast of Central America were probably produced by some change which forbade the intermingling of the inhabitants of the two provinces. At present the deep water of the tropical Pacific and the colder climate in the shallower parts of that ocean are both sufficient barriers to keep the species apart. Whether their separation was originally caused by a change of climate in higher latitudes, or by a depression in some part of the bottom of the tropical Pacific, or by the working of both of these factors, it is, of course, impossible to say.

The relations of *Pyrula decussata* with *P. papyratia* are probably more certain. In the Oligocene and Miocene the Pyrulas with the generalized apex had a free passage between the Atlantic and Pacific basins, and there was no differentiation into two geographical provinces. With the close of the Miocene the land barrier of the Isthmus of Panama was thrown up, the two oceans were separated and two geographical provinces created. After this the forms of the eastern waters, for some unknown reason, followed out a line of evolution which was chiefly marked by apical modifications, while the Pacific forms changed slightly in the cancellated stage but retained the old Miocene type of apex.

Perhaps the most important points emphasized by this study are the following: (1) We may have living at any one time on the earth's surface an assemblage of closely related gastropod species which differ to a marked degree in the evolutional grades which they have attained.

(2) *In a group of closely related gastropod species the chief modifications which are introduced with the passage of time may occur mainly in the features of the early whorls, while the later adult whorls may remain relatively unchanged.*

(3) In this particular group of species the differences in the apical characters cannot be used for the division of the assemblage into separate genera,[11] but are of use only as aids to specific discrimination, and then only when the characters of the later whorls are considered together with those of the apex.

Explanation of Plate XVII.

Fig. 1.—Apex of *Pyrula papyratia* Say. Recent. Lee County, Fla. Shows the smooth stage restricted to the large and swollen first whorl. The cancellated stage starts with the beginning of the second whorl. Greatest diameter = 3.2 mm.

Fig. 2.—Apex of *Pyrula papyratia caloosahatchiensis*. Pliocene. Caloosahatchie River, Fla. Here the cancellated stage is hardly as accelerated as in fig. 1. Greatest diameter = 3.2 mm.

Fig. 3.—Apex of *Pyrula pilsbryi duplinensis*. Miocene. Duplin County, N. C. The smooth stage occupies about 1.5 whorls. Here the initial whorl is smaller than in figs. 1 and 2.

Fig. 4.—Apex of *Pyrula pilsbryi* n. s. Oligocene (or Miocene). Bowden, Jamaica. Smooth stage occupying about 1.75 whorls. Greatest diameter = 3 mm.

Fig. 5.—Apex of *Pyrula mississippiensis* Con. Oligocene. Vicksburg Beds, Vicksburg, Miss. Here the initial whorl is much smaller than in *P. pilsbryi* and the smooth stage extends over three whorls. Greatest diameter = 3.5 mm.

Fig. 6.—Apex of *Pyrula filia* Meyer. Eocene. Jackson Beds, Jackson, Miss. Smooth stage of about 2.5 whorls. Greatest diameter = 3.5 mm.

Fig. 7.—Apex of *Pyrula decussata* Wood. Recent. Acapulco. Smooth stage of about 2 whorls. Greatest diameter = 2.8 mm.

Fig. 8.—Apex of *Pyrula dussumieri* Valenc. Recent. China. Smooth stage of about 1.6 whorls. Greatest diameter = 3 mm.

Fig. 9.—Apex of *Pyrula ficus* Linn. Recent. East Indies. Smooth stage of about 1.7 whorls. Greatest diameter = 2.6 mm.

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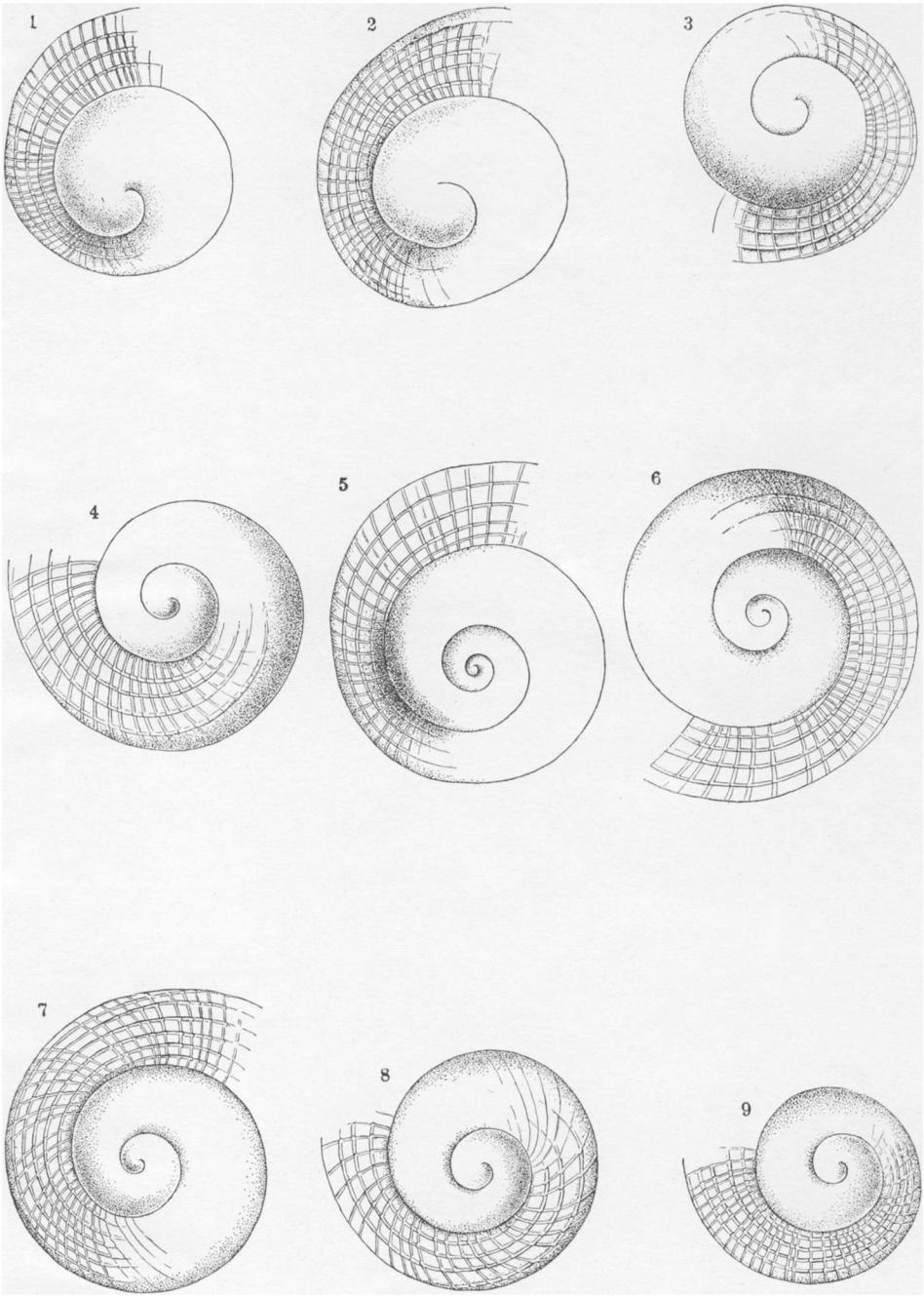
[11] See *Proc. Linn. Soc. New South Wales*, 1905, Pt. II, p. 325, "Notes on Prosobranchiata, No. IV—The Ontogenetic Stages represented by the Gastropod Protoconch," by H. Leighton Kesteven. On p. 334 he says: "The protoconch is to be used in conjunction with other features, and that only where the other features, anatomic or conchological, are negative or unknown is it to be used in deciding a systematic position or generic segregation."



BURNETT SMITH ON PYRULA.